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THE OSTEOLOGY AND RELATIONSHIPS OF THE ROUND HERRING

Etrumeus micropus Temminck and Schlegel

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THE ROUND herrings are a small group of fishes found in tropical and temperate parts of the Atlantic, Pacific, and Indian oceans. They are sometimes included in the Clupeidae and sometimes segregated into a separate family, the Dussumieridae. The brief discussion of the skull of *Dussumieria acuta* by Ridewood (1904) is the chief source of information on the osteology of the group. To the writer's knowledge no study of the anatomy of the genus *Etrumeus*, or of the axial skeleton of any of the group, has been previously made. It is the purpose of the present report to describe the osteology of *Etrumeus micropus* Temminck and Schlegel and discuss the relationships of the round herrings to the other Clupeoid fishes.

CRANIUM

The cranium (Figs. 1, 2, and 3) bears a strong resemblance to that of the Clupeidae (Figs. 4, 5, and 6; and Phillips, 1942), but differs in the following respects: The ethmoid cartilage is considerably broader and bulkier between the prefrontals and the anterolateral wings of the mesethmoid. The ossification of the mesethmoid is correspondingly reduced in size. There is no foramen in the cartilage which is exposed dorsally between the anterior ends of the frontals. The anterior knob of the vomer is proportionately enlarged and bears teeth, while the posterior shank of the bone is broader than in the Clupeidae, and not so long.

The orbitosphenoid arches high under the frontals, without an opening between it and the cartilage, except the foramina for the emergence of the

olfactory nerves. The anterior end is broad and curves downward behind the prefrontal to reach the cartilage over the parasphenoid, not as shown by Ridewood (1904, Fig. 131) for *Dussumieria acuta*. No median wing was found descending from the small basisphenoid to the parasphenoid.

The lateral projection of the sphenotic is much smaller than in the Clupeidae. The temporal foramen is a small slit. The epiotic fossa is deep and large, but scarcely visible in dorsal aspect. More of the supraoccipital is exposed between the parietals than in the Clupeidae. The sockets of articulation of the hyomandibular are separate, one on the pterotic, the other on the sphenotic. The auditory foramen is entirely borne by the exoccipital.

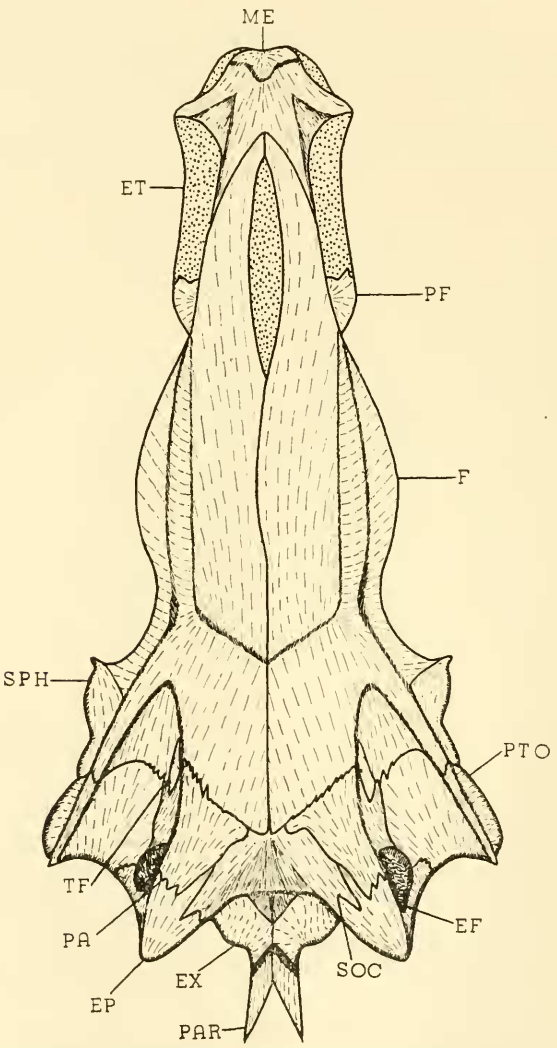

Fig. 1.—Dorsal view of the cranium of *Etrumeus micropus*. x4

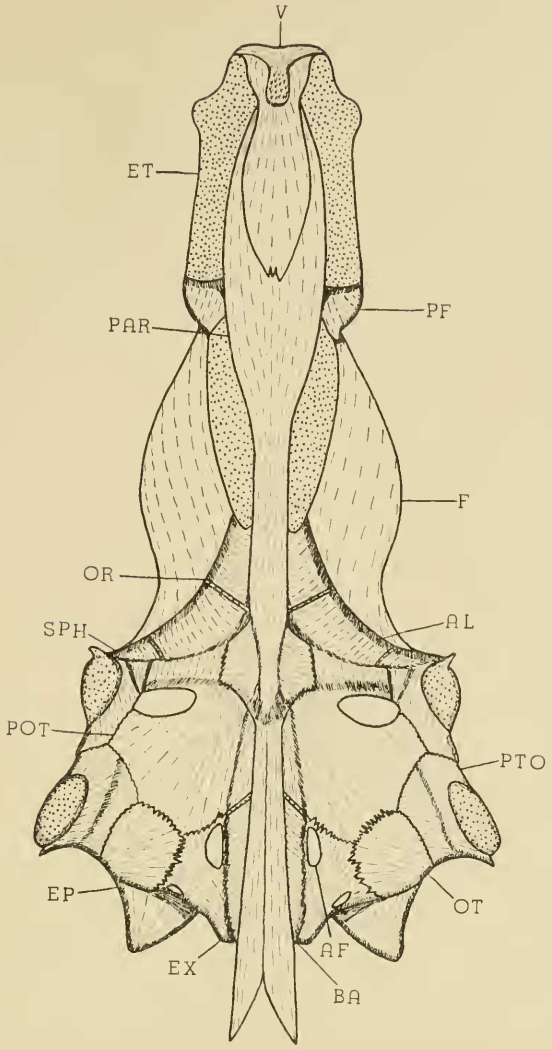

FIG. 2.—Ventral view of the cranium of *Etrumeus micropus*, x4

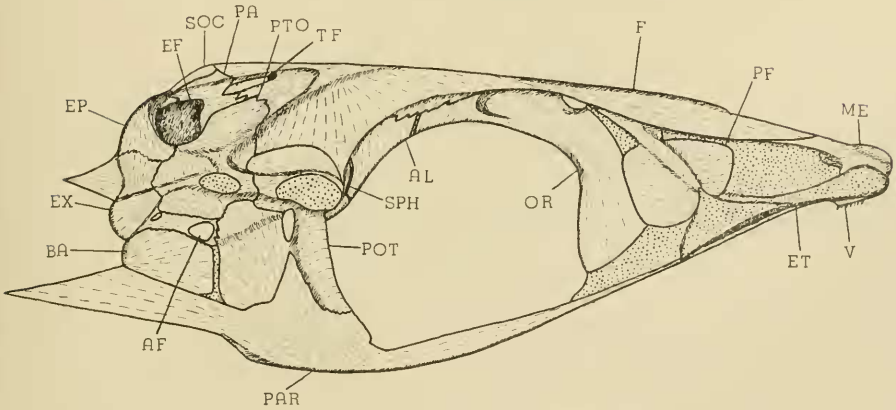

FIG. 3.—Lateral view of the cranium of *Etrumeus micropus*, x3.5

Special Ossifications of the Sensory System

The nasal (Fig. 7) is a thin, flat bone with about the same surface area as the second circumorbital bone. It lies directly over the nasal capsule and, while it bears the anterior portion of the sensory nerve, it is not grooved nor tubular for the protection of the nerve, and is only slightly concave on top.

The seven bones of the circumorbital series of the Clupeidae are found here (Fig. 7), but in somewhat differing proportions. The anterior half of the first is broadened and flattened in a vertical plane. The second is likewise broadened, with its dorsal edge overlying the ventral edge of the first, and

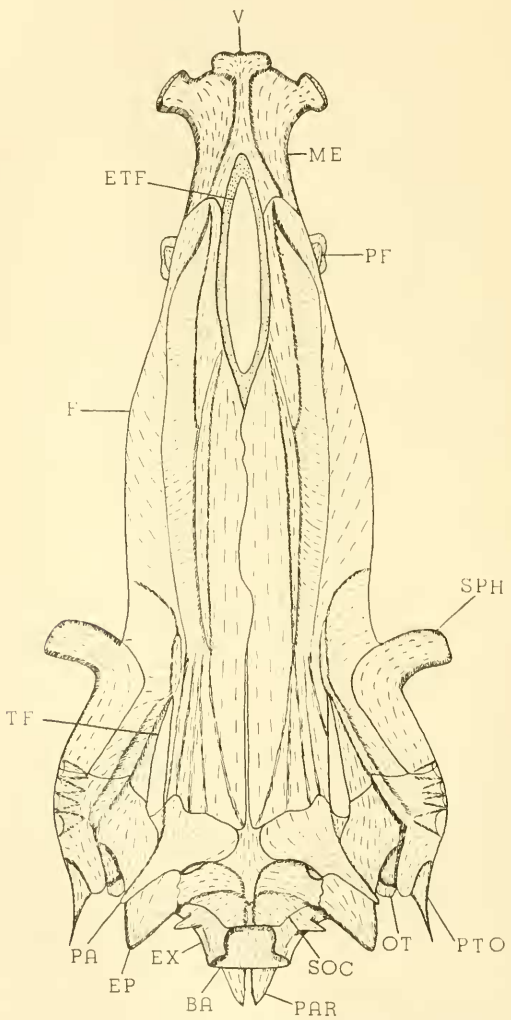

Fig. 4.—Dorsal view of the cranium of *Sardinops caerulea*, x2.5

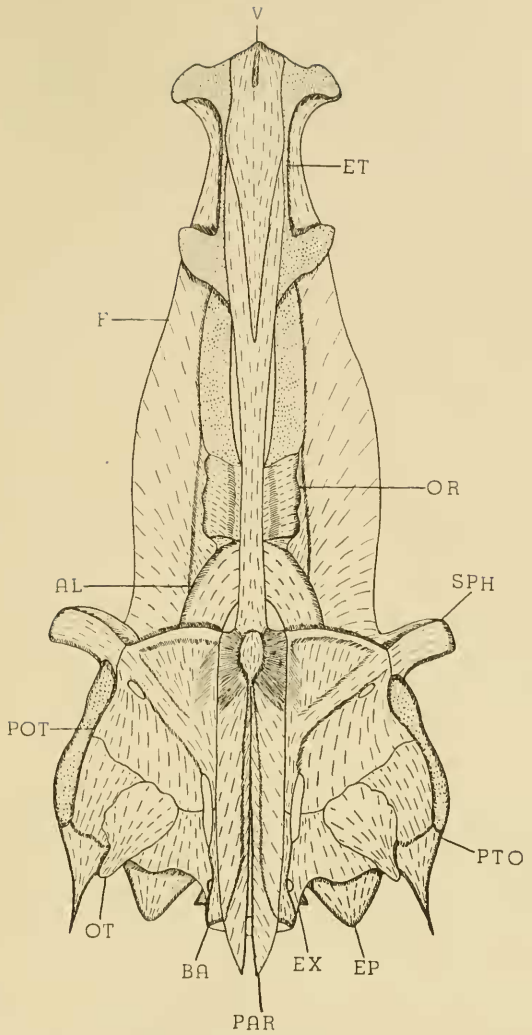

FIG. 5.—Ventral view of the cranium of *Sardinops caerulea*, x2.5

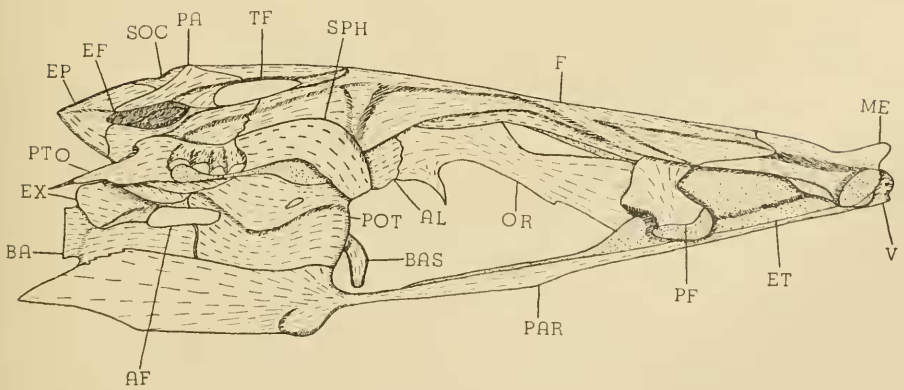

FIG. 6.—Lateral view of the cranium of *Sardinops caerulea*, x2

slightly underlying the dorsal edge of the third (lachrymal). The fifth is proportionately even larger than in the Clupeidae. Its posterior edge, together with the sixth and seventh bones, overlie the preopercle, leaving no interosseous space. A thin tubular bone, not illustrated, bridges the gap between the pterotic and posttemporal.

Upper Jaw

The premaxillary (Fig. 7) is smaller than in the Clupeidae and is without teeth. The lateral face of the maxillary bears a longitudinal ridge which in life meets the lower edge of the lachrymal, leaving the dorsal edge of the maxillary and the supramaxillary hidden under the circumorbital bones. The maxillary bears a single row of tiny teeth. There is a single, slender supramaxillary.

Lower Jaw

The mandible is deepest over its posterior third. The dentary (Fig. 8) bears a single row of teeth, which are larger than those on the maxillary. The small angular is almost covered laterally by the posterior prong of the articular. The sesamoid articular is a tiny, thin bone lying against the angular and over the posterior end of Meckel's cartilage. The latter is a slender straight rod of cartilage extending from the middle of the angular to the anterior third of the dentary. The angular is broadly overlapped by the dentary.

Palatine Arch

The palatine (Fig. 8) is long and slender and bears a plate of fine teeth (like those on the tongue) along its under and inner surface. The pterygoid is a thin bone, mostly in a vertical plane, which lies over the cartilage behind the palatine and that between the quadrate and mesopterygoid. It does not bear teeth, although the posterior projection of the palatine, which overlies the anterior end of the bone and does bear teeth, gives it the appearance of doing so. From the dorsal end of the bone, but borne mostly on the carti-

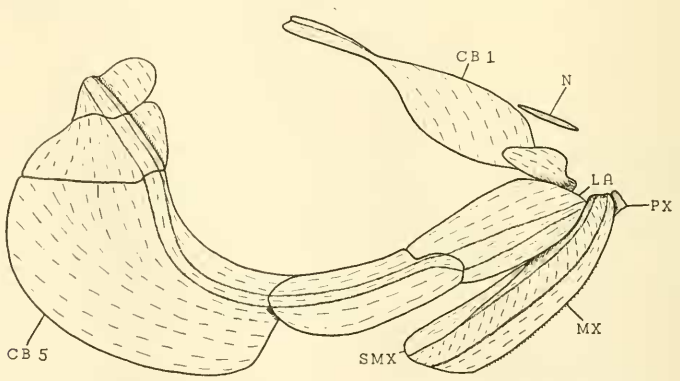

Fig. 7.—Circumorbital bones and upper jaw of *Etrumeus micropus*, x3

lage, a tough tendon runs to the cavity in the posterior side of the frontal above, and securely binds the palatine arch to the cranium. The mesopterygoid is long and thin and extends far forward along the inner side of the palatine nearly to the anterior end of that bone (as shown by Ridewood, 1904, Fig. 132, for *Dussumieria acuta*). Excepting the posterior quarter of its surface, the under side of the bone is entirely covered by fine, almost granular, teeth. The dorsal side of the bone is slightly concave and supports the eye. A small projection from the inner edge of the metapterygoid aids in supporting the posterior end of the mesopterygoid. Behind the mesopterygoid lies another bone of the same nature which is broader than the mesopterygoid and has almost as much surface area. It lies under the toothless posterior end of the mesopterygoid and extends posteriorly under the metapterygoid and hyomandibular. It lies loosely in the membranes of the roof of the mouth and is not associated with the other bones. A considerable thickness of membranes lies between it and the mesopterygoid. The under side of the bone is completely covered with fine teeth. This bone is not shown by Ridewood for *Dussumieria*. It has been found in the Engraulidae, but not the Clupeidae (Chapman, 1943, *a* and *b*).

The metapterygoid (Fig. 8) is proportionately smaller than in the Clupeidae, but it is a strongly ossified bone. There is a characteristic interosseous space between it and the ventral edge of the hyomandibular. The quadrate differs little from that of the Clupeidae.

Hyoid Arch

The hyomandibular (Fig. 8) has two distinct cranial condyles, of which the posterior one is a little the larger. The anterior condyle articulates entirely on the sphenotic; the posterior entirely on the pterotic. The opercular condyle

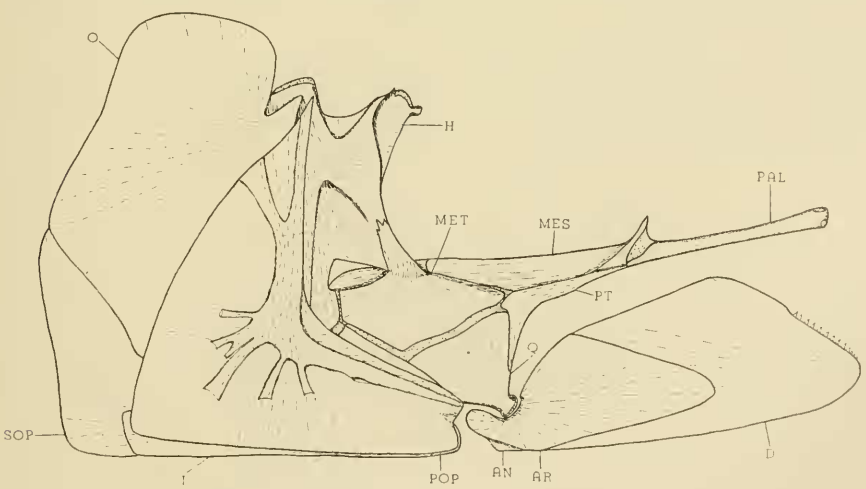

Fig. 8.—Lateral view of the suspensorium of *Etrumeus micropus*, x3

curves downward from the posterior condyle and is about the same size as the anterior condyle. The hyoido-mandibularis facialis nerve enters the bone on the inner side near the top of the anterior condyle and emerges through a broad opening near the center of the face of the bone. The anterior side of the ventral edge of the bone is suturally connected with a strong spur projecting up from the metapterygoid. The ventral edge of the bone is characteristically cut away, leaving a large opening between the hyomandibular and the metapterygoid. The long, slender sympletic extends anteroventrally at an angle of about 120° with the hyomandibular.

The tiny, conical interhyal (Fig. 9) is attached to the pad of cartilage

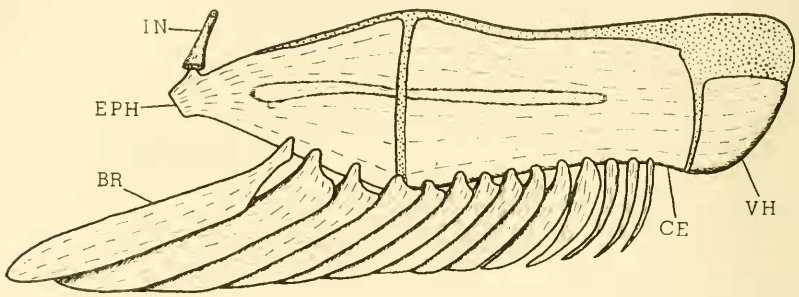

Fig. 9.—Hyoid apparatus of *Etrumeus micropus*, x4

between the hyomandibular and the symplectic and is attached ventrally to a slight protuberance from the epihyal. The ventral edge of the ceratohyal (Fig. 9) is not excavated as in the Clupeidae, but the groove in the middle of the epihyal and ceratohyal, characteristic of the Clupeidae, is found here. The dorsal hypohyal is not visible from the lateral aspect (Fig. 9), since it is covered with cartilage, but it is only a little smaller than the ventral hypohyal. There are a great many more branchiostegal rays (14) than in the Clupeidae, but they are considerably smaller. The loss of branchiostegal rays in the Chupeidae has been mainly from those articulating with the ceratohyal.

Opercular Apparatus

The opercle, subopercle, and interopercle (Fig. 8) differ only in relative proportions from the same bones in Clupeidae, except that the extensions of the sensory system over the opercle, which more or less mark the Clupeoid opercle, are not present here. The preopercle is broadly expanded posteriorly, quite unlike that of the Clupeidae; has numerous subsidiary tubules coming off the main nerve tube; nearly covers the interopercle, and leaves no open space between the preopercle and the other opercular bones. Rather than being of the customary boomerang shape, the preopercle is almost triangular in lateral view.

Gill Arches

The lower half of the gill arch (Fig. 10) is well supplied with small granular teeth, which work against those of the roof of the mouth. The

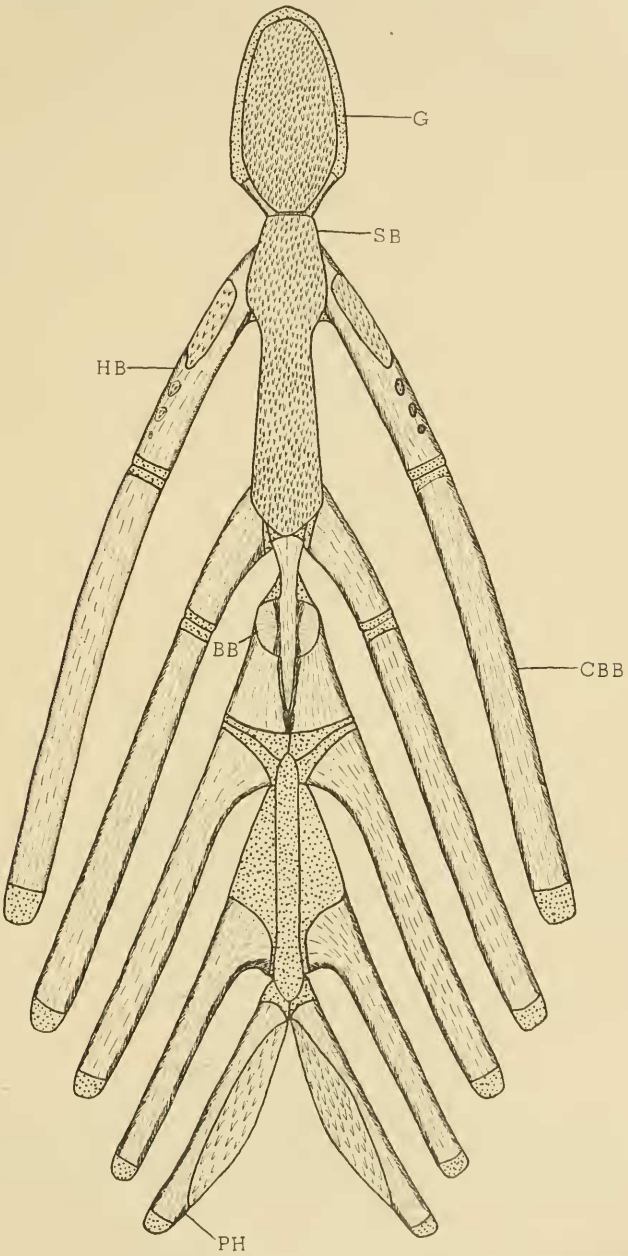

Fig. 10.—Dorsal view of the ventral half of the gill arches of *Etrumeus micropus*, x4

glossohyal is large, but mostly cartilaginous. It is nearly covered dorsally by a thin plate of teeth. The suprabasal bone, found so well developed in the Engraulidae, Osmeridae, and Plecoglossidae, but poorly developed and edentulous in the Clupeidae (Fig. 11), covers the first two basibranchials and is completely covered with teeth. There are small patches of teeth on separable bony plates on the hypobranchials of the first gill arch. The teeth of the anterior part of the gill arch work against those on the vomer, palatines, and

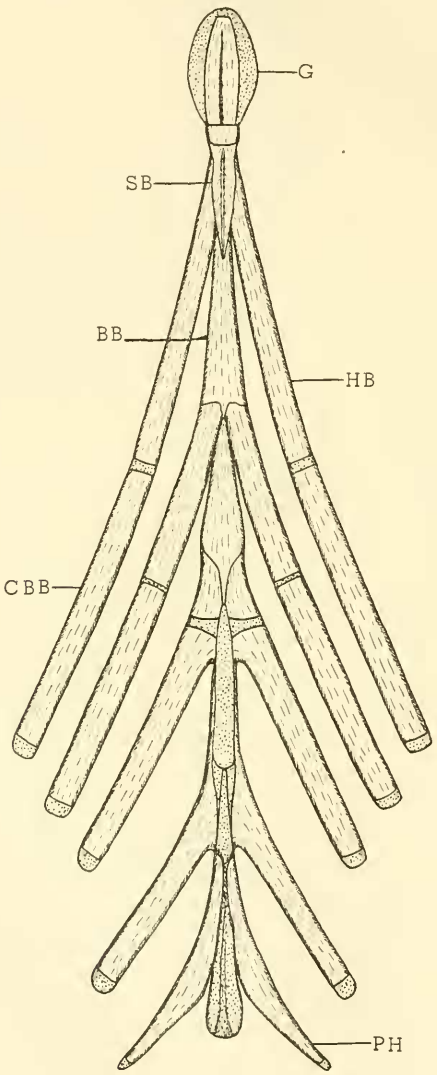

Fig. 11.—Dorsal view of the ventral half of the gill arches of *Sardinops caerulea*, x2

mesopterygoids above, although those on the palatines are more in apposition to those on the dentaries. The pharyngeals and fourth suprabranchials (Fig. 12) likewise bear plates of teeth which oppose each other. They are somewhat larger and not so thickly concentrated as those in the front of the mouth. There are no teeth dorsally on the first three gill arches (Fig. 12). The gill rakers (Fig. 13) are shorter, stubbier, and less numerous than is typical for the Clupeidae (Fig. 14).

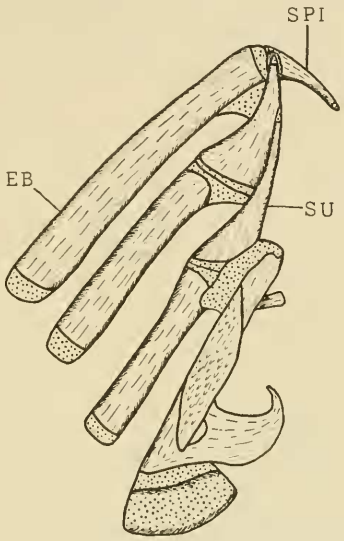

Fig. 12.—Ventral view of the dorsal half of the gill arches of *Etrumeus micropus*, x4

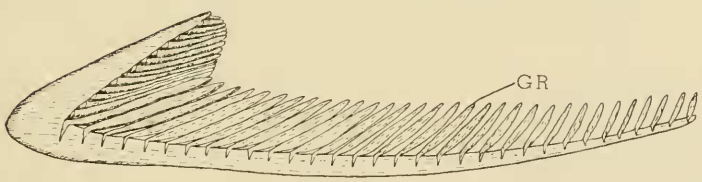

Fig. 13.—Lateral view of the gill rakers on the first arch of *Etrumeus micropus*, x4

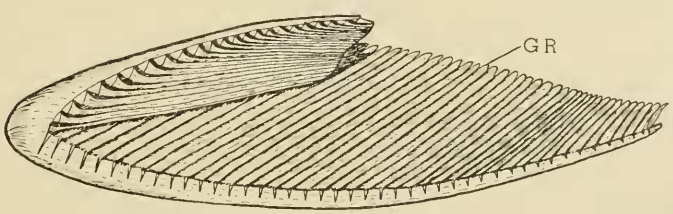

Fig. 14.—Lateral view of the gill rakers on the first arch of *Alosa sapidissima*, x4

Pectoral Girdle

The posttemporal (Fig. 15) is not as strong as in the Clupeidae (Fig. 16). The flattened body of the bone is smaller and both the epiotic and opisthotic arms are longer and more slender. The supracleithrum, on the other hand, is longer and considerably wider than in the Clupeidae. It bears a short tube for the lateral line nerve on its outer face. There are two postcleithra: the first a simple flat bone, shaped like a scale, which is fitted in between the supracleithrum and cleithrum, and the second, which has a long spine projecting posteroventrally like that of *Sardinops* (Fig. 16), although the spine is not so long or heavy as in the sardine.

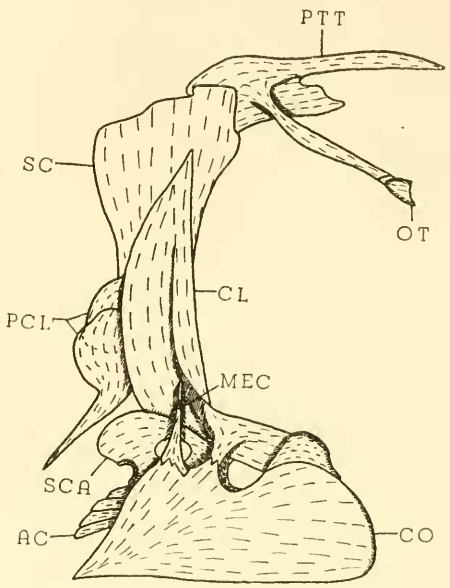

Fig. 15.—Mesial view of the shoulder girdle of *Etrumeus micropus*, x3

The mesocoracoid is slender and attached dorsally to the anterior edge of the inner side of the cleithrum. The coracoid is proportionately larger and more heavily ossified than in the Clupeidae. The anterior edge is particularly broadly expanded. The interosseous opening between the cleithrum and coracoid is about three times the size it is in *Sardinops*. Behind this opening the coracoid is suturally attached to a process from the inner side of the cleithrum. The shoulder girdle is otherwise much as in *Sardinops*.

Pelvic Girdle

The pelvic bones (Fig. 17) are triangular and considerably broader and larger than in the Clupeidae. The chief feature of the pelvic girdle is the two modified ventral scutes which are much broadened and probably serve to help

distribute the stresses of the movement of the fin. These are the only ventral scutes present on the abdomen.

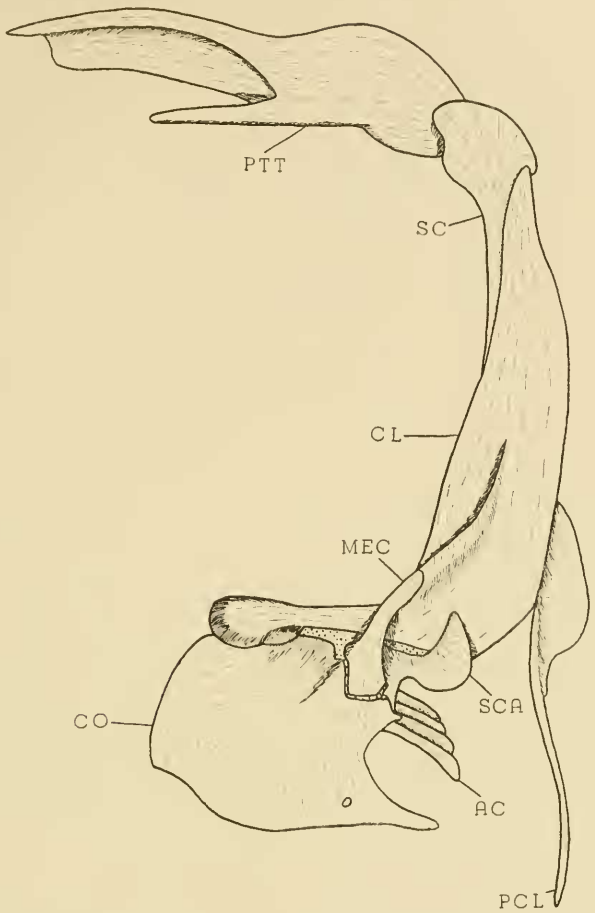

Fig. 16.—Mesial view of the shoulder girdle of *Sardinops caerulea*, x2.5

Axial Skeleton

In one specimen of *Etrumeus* there were 56 vertebrae, including the terminal centrum. The haemal arch is closed first on the 18th vertebra. On this vertebra the parapophyses, whose union on the posterior caudal vertebrae forms the haemal arch and spine, are short, and not as deep as the centrum. The parapophyses get only slightly larger back to the 29th vertebra, but posterior to that they become increasingly lengthened until the 41st vertebra is reached. All of the first 41 vertebrae bear pleural ribs, which are all attached ligamentously to the parapophyses. On the last ten of these vertebrae the ribs are very loosely attached. The parapophyses throughout the abdomen are

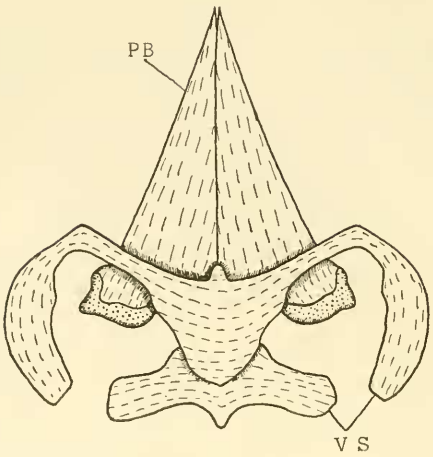

Fig. 17.—Ventral view of the pelvic girdle and supporting ventral scutes of *Etrumeus micropus*, x3

proportionately longer than those of the Clupeidae, and the ribs are broader. The anterior haemal zygapophyses appear first on the 31st vertebra; the anterior neural zygapophyses on the 25th. Anterior to this point the posterior neural zygapophysis is a blunt hump on the vertebra which does not overlap the following centrum, but by the time the 35th vertebra is reached this process has diminished in size until it is nearly lost. The posterior haemal zygapophysis retains its identity for another five vertebrae posteriorly, but then becomes only a point on the back of the vertebra. It does not project strongly ventrally as in the Engraulidae. The anterior zygapophyses of the caudal vertebrae (Fig. 18) are long, slender, and hug tightly the preceding vertebrae as in *Opisthonema* and *Sardinops*, though they are more slender and spikelike than in those genera. The anterior haemal zygapophysis of the penultimate vertebra is characteristically enlarged. Hypural number 4 is characteristically

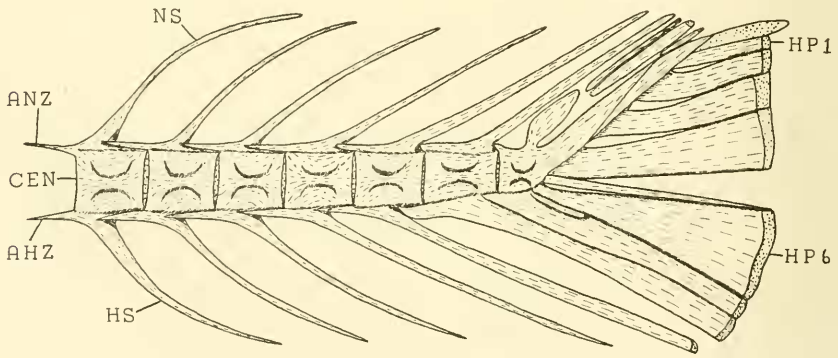

Fig. 18.—Caudal skeleton of *Etrumeus micropus*, x4

narrower than in the Clupeidae and hypural number 5 is slender and tapers posteriorly (unlike in the Clupeidae).

All of the neural spines anterior to, and under, the dorsal fin are very slender and are not united dorsally, the first one behind the dorsal fin being the first in which the two halves are united dorsally into a stiff spine. The first interneural is enlarged, lengthened and broadened, and extends down past the first neural spine to lie over the foramen magnum and protect the spinal nerve as it emerges from the cranium. The remaining interneurals are all much heavier than the adjacent neural spines. There are nineteen pterygiophores for the support of the dorsal fin. The first is very broadly expanded and the next five or six bear lateral vanes of bone which permit a broader attachment for the fin musculature. The series terminates in the long, slender dorsal stay typical of the Clupeoid fishes. The twelve pterygiophores of the anal fin are closely bunched together under the haemal spines of the 42d to 45th vertebrae. The first is somewhat broadened, but the rest are very long and slender, the twelfth little shorter than the second.

Epineurals and epipleurals are present on all vertebrae as in the Clupeidae, but those over the posterior part of the abdomen are branched several times instead of bearing a single fork as in the Clupeidae. On the caudal peduncle these bones are broadened and form an almost continuous bony sheath under the skin. Long, slender, simple epicentrals are present on all vertebrae in distinction to the condition in the Clupeidae and Engraulidae where they are absent on most of the caudal vertebrae. There are no myorhabdoi either dorsally or ventrally. The only ventral scutes present are the two associated with the support of the pelvic fins. In the anterior segments the backward radiating osseous brushes from the epiotic region of the cranium fill the place of the epineurals, which they resemble, except that they are even more slender, and more numerous. They are not grouped in bunches as in the Clupeidae.

Discussion

While the round herrings, of which *Etrumeus* is one, are often associated with the Clupeidae, and never with the Engraulidae, they nevertheless share several peculiar osteological characters with the latter (Chapman, 1943*b*) which are not found in the Clupeidae (Phillips, 1942; Chapman, 1943*a*). Among these are: (1) the possession of the toothed secondary mesopterygoid; (2) the well-developed, toothed suprabasal bone over the first two basibranchials; (3) the bifurcated, dorsal articular head of the hyomandibular; (4) the lack of a descending limb on the basisphenoid; (5) the numerous branchiostegal rays; and (6) the lack of ventral scutes, save for one or two remaining in the pelvic region. The first, second, and fifth of these characters must be considered primitive and are evidence that the round herrings are of ancient derivation and, rather than being a specialized offshoot of the Clupeidae, had already differentiated from the primitive Clupeoid stock before the development of recent Clupeidae. This is further borne out by the retention of epi-

centrals on all caudal vertebrae (lost on the posterior caudal vertebrae in the Clupeidae and Engraulidae), the presence of two postcleithra, and the primitive, simple condition of the various bony processes radiating back into the body musculature from the back of the cranium.

There is no indication, however, that the round herrings bear a close relation to recent Engraulids, for they share none of the striking specializations of that group, such as the enormous gape with its attendant osseous changes, the development of the cross-struts on the frontals, the exceptional development of the intermuscular bones of the body, and the large and prominent mesethmoid. The evidence is simply that both groups retain certain characters of the ancestral Clupeoid stock which recent Clupeids have lost.

The above-noticed characters, the rounded abdomen, the abbreviated anal fin, the posterior insertion of the pelvic fins, the complete fusion of the adipose eyelids over the eyes, and other characters cited in the text serve to show that these fishes are as deserving of familial status as the Engraulidae or Clupeidae. They comprise the family Dussumieridae.

Diagnosis of the Family Dussumieridae

Clupeoid fishes with a single supramaxillary; fifth bone of circumorbital series very large, not cut away anteriorly, and with its posterior edge overlying the preopercle; hyomandibular with two separate cranial heads, one for the sphenotic and the other for the pterotic articulation; ventral edge of the hyomandibular cut away so that there is an open space between it and the metapterygoid; preopercle broadly expanded posteroventrally so as to cover most of interopercle and its junction with the subopercle; gape small, not reaching behind eye; glossohyal large and covered with fine teeth; suprabasal long and broad, covering first two basibranchials and covered with fine teeth; two mesopterygoids, both covered with teeth; ceratobranchial of fifth gill arch with a long pad of small teeth; teeth found dorsally only on fourth gill arch; no ethmoid foramen; no median descending wing on basisphenoid; two postcleithra present; anterior zygapophyses very strongly developed in caudal region, and broadly overlapping the preceding vertebra; ventral scutes absent except for two in region of pelvic fin insertion; myorhabdoi absent both dorsally and ventrally; epicentrals present on all vertebrae; posterior haemal zygapophyses short throughout, and not projecting strongly on posterior abdominal vertebrae; pelvic fins behind dorsal; belly smoothly rounded; anal fin much shorter than dorsal; adipose layer over eye continuous, without vertical slit over pupil.

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ABBREVIATIONS USED IN ALL FIGURES

AC	Actinost
AF	Auditory foramen
AHZ	Anterior haemal zygapophysis
AL	Alisphenoid
AN	Angular
ANZ	Anterior neural zygapophysis
AR	Articular
BA	Basioccipital
BAS	Basisphenoid
BB	Basibranchial
BR	Branchiostegal ray
CB	Circumorbital
CBB	Ceratobranchial
CE	Ceratohyal
CEN	Centrum
CL	Cleithrum
CO	Coracoid
D	Dentary
EB	Epibranchial
EF	Epiotic fossa
EP	Epiotic
EPH	Epihyal
ET	Ethmoid cartilage
ETF	Ethmoid foramen
EX	Exoccipital
F	Frontal
G	Glossohyal
GR	Gill raker
H	Hyomandibular
HB	Hypobranchial
HS	Haemal spine
I	Interopercle
IN	Interhyal
LA	Lachrymal
ME	Mesethmoid
MEC	Mesocoracoid
MES	Mesopterygoid
MET	Metapterygoid
MX	Maxillary
N	Nasal
NS	Neural spine
O	Opercle
OR	Orbitosphenoid
OT	Opisthotic
PA	Parietal
PAL	Palatine
PAR	Parasphenoid
PB	Pelvic bone
PCL	Postcleithrum
PF	Prefrontal
PH	Pharyngeal
POP	Preopercle
POT	Pro-otic
PT	Pterygoid
PTO	Pterotic
PTT	Posttemporal
PX	Premaxillary
Q	Quadrate
SB	Suprabasal
SC	Supracleithrum
SCA	Scapula
SMX	Supramaxillary
SOC	Supraoccipital
SOP	Subopercle
SPH	Sphenotic
SPI	Spicular
SU	Suprabranchial
TF	Temporal foramen
V	Vomer
VH	Ventral hypohyal
VS	Ventral scute